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# Geographic Variation and Succession of Arthropod Communities in Inflorescences and Infructescences of *Xanthosoma* (Araceae)[1]

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## ABSTRACT

Phytotelmata, small aquatic ecosystems within different structures of terrestrial plants, occur in the inflorescescences and infructescences of *Xanthosoma* (Araceae). This study reports changes in composition and abundance of arthropods during the anthesis of inflorescences and in the developing infructescences of three species of *Xanthosoma* at three different geographic locations*:* (1) *X. undipes* in a tropical cloud forest of Costa Rica, Central America; (2) *X. daguense* in a tropical cloud forest in the central Andes of Colombia; and (3) *X. poeppigii* in the Peruvian Amazonas. All *Xanthosoma* species displayed similar interactions with the main pollinators, dynastine beetles. We observed a succession from terrestrial to aquatic arthropods as inflorescences aged and set fruit. However, community composition varied among different *Xanthosoma* species. Some arthropods recorded in *Xanthosoma* phytotelmata have also been reported as inflorescence visitors of the dynastine-pollinated terrestrial genus *Dieffenbachia* and of vines from *Philodendon* and *Syngonium*. Further research may elucidate if phytotelmata similar to those described for *Xanthosoma* could occur among dynastine-pollinated genera of Araceae, both in the understory and the canopy of Neotropical forests.

## RESUMEN

Las fitotelmata, pequeños ecosistemas contenidos dentro de diversas estructuras de plantas terrestres, están presentes en inflorescencias e infrutescencias de *Xanthosoma* (Araceae). Este estudio reporta los cambios en la composición y abundancia de artrópodos durante la antesis de inflorescencias, y la fructificación en tres especies de *Xanthosoma* presentes en tres diferentes localidades geográficas: 1) *X. undipes*, presente en un bosque montano en Costa Rica, América Central; 2) *X. daguense* presente en un bosque montano en los Andes centrales de Colombia, Sur América; y 3) *X. poeppigii* en la Amazonia peruana en Sur América. Las tres especies de *Xanthosoma* presentaron interacciones similares con sus polinizadores, escarabajos dynástinos. Las inflorescencias, inicialmente colonizadas por artrópodos terrestres, al marchitarse y producir frutos, presentaron un proceso de sucesión y posterior colonización por artrópodos acuáticos. Sin embargo, la composición de artrópodos varió entre las tres especies de *Xanthosoma.* Algunos de los artrópodos registrados en fitotelmata de *Xanthosoma* también han sido reportados como visitantes de inflorescencias en el género terrestre *Dieffenbachia* y bejucos de los géneros *Philodendron* y *Syngonium.* Futuras investigaciones podrían dilucidar si sistemas similares al descrito para *Xanthosoma* son comunes en la familia Araceae, tanto en el sotobosque como en el dosel de los bosques Neotropicales.

*Key words: arthropod communities; geographic variation; phytotelmata;* Xanthosoma.

PHYTOTELMATA ARE SMALL AQUATIC ECOSYSTEMS located in different structures of terrestrial plants and shelter complex communities of invertebrates (Frank & Lounibos 1983). In these ecosystems, biotic and abiotic dynamics occur over very short periods of time compared with other aquatic ecosystems because turnover rates of phytotelmata depend on the lifespans of plant structures (Frank & Lounibos 1983, Kitching 2000). These phytotelmata ecosystems and the communities inhabiting them may persist from a few days to several months or years (Kitching 2000).

Structures providing chambers suitable for phytotelmata communities include elongated leaf axils as in Strelitziaceae, certain palms, *Pandanus* (Pandanaceae), and *Xanthosoma* (Araceae) (Kitching 2000), and tank bromeliads (Bromeliaceae; Picado 1913, Laessle 1961, Frank 1983, Kitching 2000). In pitcher plants such as *Nepenthes* (Nepenthaceae) and *Sarracenia* (Sarraceniaceae), modified leaves used to capture insects are also inhabited by organisms adapted to the conditions inside these insect traps (Fish & Hall 1978; Beaver 1983, 1985). Other structures that become filled with water include hollow stems in *Guadua weberbaueri* (Poaceae, Bambusoideae; Louton *et al.* 1996), tree cavities, and rotten trunks (Park *et al.* 1950, Kitching 2000).

Flowers and bracts also occasionally fill with water. Families forming phytotelmata in these structures include Gesneriaceae, Marantaceae, Rafflesiaceae, Strelitziaceae, Zingiberaceae, and Heliconiaceae (Beutelspacher & Butze 1975; Seifert 1975, 1982; Bronstein 1986; Harvey 1988; Naeem 1990; Lounibos and Machado-Allison 1993; Kitching 2000). These may be the most dynamic types of phytotelmata due to the ephemeral but fixed lifespan of the plant structure containing the community. Consequently, arthropods must adapt to the flowering dynamics, turnover rates, and changes in nutrient inputs of these plants to be successful colonizers (Barrera & Medialdea 1996, Kitching 2000).

Inflorescences in *Xanthosoma* (Araceae) provide shelter to communities of arthropods (Goldwasser 2000, García-Robledo *et al.*

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2004). An inflorescence is composed of a spadix with pistilate flowers at the base, a belt of sterile flowers offered as a reward for pollinators in the middle, and staminate flowers on the upper part (García-Robledo *et al.* 2004). Prior to opening, the inflorescence is enclosed within a leaf-like spathe. When the flowers are ready to open, the upper part of the spathe opens and exposes the staminate area of the spadix; the basal area of the spathe remains closed, forming a spacious chamber, the spathe tube, which encloses the pistilate and sterile flowers (García-Robledo *et al.* 2004). These spathe tubes could be filled with rainwater, forming phytotelmata.

The spathe tube also has a very important function during the specialized nocturnal pollination by dynastine beetles typical of *Xanthosoma* (García-Robledo *et al.* 2004, García-Robledo *et al.* 2005). In the species under consideration in this study, the flowering process lasts for only two nights. Inflorescences open during the night, increasing the temperature inside the spathe tube and producing a sweet scent in order to attract the pollinators, Dynastinae beetles (Goldwasser 2000, García-Robledo *et al.* 2004). Dynastine beetles arrive, covered with pollen from another inflorescence, and remain within the spathe tube for 24 h, leaving abundant pollen in the inner walls of the chamber and over the stigmas (García-Robledo *et al.* 2004). Inside the spathe tube, dynastines mate and feed on the belt of sterile flowers (García-Robledo *et al.* 2004; C. García-Robledo, pers. obs.). On the second night, the beetles emerge from the tube and walk over the staminate flowers, becoming covered with pollen. Thereafter, they fly to a recently opened inflorescence (Fig. 1a).

After anthesis, the spathe tube always remains open, and may become filled with rainwater, forming a dense mixture of water and pollen. Subsequent to this, different arthropods begin colonization. After 3 d, the upper portion of the spadix starts to decay and finally fall off; however, the spathe tube remains (Fig. 1b). If pollination fails, inflorescences abort after a few days and arthropods within the inflorescence must migrate in order to survive (García-Robledo *et al.* 2004). However, if pollination is successful, the community can persist within the shelter of the spathe tube through the course of several months until the infructescence develops completely (Fig. 1c and d; García-Robledo *et al.* 2004).

Despite the unique characteristics of this ecosystem, there have been no previous descriptions of the composition and succession dynamics of the arthropod communities in inflorescences and infructescences of *Xanthosoma*. The objectives of this research are to: (1) document the fauna associated with phytotelmata in inflorescences and infructescences of *Xanthosoma*, determining the changes in composition and abundance of arthropods during the flowering and fruiting phases; (2) describe the variation in composition and abundance of arthropods associated with inflorescences and infructescences of *Xanthosoma* among species and at a broad geographic scale. In order to attain these objectives, we recorded the successional processes of arthropods associated with three species of *Xanthosoma*, in populations located in three distant localities in the tropical cloud forests of Costa Rica and Colombia, and the tropical lowland forest in the Peruvian Amazonas.

FIGURE 1. Flowering and fruiting in *Xanthosoma.* (a) Inflorescence visited by pollinators, *Cyclocephala gregaria*; (b) staminate area of the spadix, and spathe blade falling after 3 d of anthesis; (c) developing infructescence; and (d) spathe tube starting to open and displaying ripe fruits (Pictures: *X. daguense* (a) by G. Londoño; (b–d) by C. García-Robledo).

## METHODS

STUDY SITES.—This study was conducted at three localities in Central and South America. The first study area was located in a tropical montane forest of Costa Rica, Prov. Cartago, Mpio. San Ramón de La Unión (9°56′N, 83°57′W, 1782 m). The second locality was a tropical montane forest in the Central Andes of Colombia, Dto. Risaralda, Mpio. Pereira, Vda. La Suiza, Santuario Otún Quimbaya (4°39′N, 75°36′W, 1900 m). The third locality was an Amazonian tropical flood forest in Peru, Dto. Loreto, Prov. Orellana, Estación Biológica Madre Selva (3°37′S, 72°14′W, 120 m).

STUDY SPECIES.—*Xanthosoma* (Araceae) is the most diverse genus of terrestrial aroids, with *ca* 45 species (Gentry 1996). *Xanthosoma* is broadly distributed from the subtropical areas in the north of Argentina to Mexico (Mayo *et al.* 1997). All species included in this study are clonal, terrestrial herbs that grow in wet areas. Ramets open only one inflorescence at a time (C. García-Robledo *et al.*, pers. obs.). In Costa Rica we studied *X. undipes* K. Koch. This species forms a pseudostem that can reach a height of 3 m. In Colombia we selected *X. daguense* Engl. (Voucher: Croat 84942, MO); this species is smaller than *X. undipes*, reaching a height of *ca* 2 m. The species studied in Peru was *X. poeppigii* Schott (Vouchers, R. Vasquez *sn*, MO). This species does not develop a pseudostem, reaching only 1 m height.

SAMPLING OF ARTHROPOD COMMUNITIES.—We sampled arthropod communities inhabiting inflorescences of *X. undipes* between July and August 2003, *X. daguense* between May and early July 2001, and *X. poeppigii* during May 2003. To record changes of arthropod composition and abundance during flowering within and among *Xanthosoma* species, we collected inflorescences after the first night of anthesis, when pollinators arrive, the second night, when pollen is produced and pollinators fly to new inflorescences, and after the third night of opening, when inflorescence starts either to decay or to produce fruits depending on success during the pollination process (see sample size in Table 1). To determine inflorescence visits by the pollinators, dynastine beetles, we recorded the number of individuals in inflorescences on the first night of opening and any indication of sterile flowers consumption in older inflorescences. Arthropods inside the spathe tubes of *X. daguense* were fixed in ethanol, and arthropod composition and abundance were determined in a laboratory. Arthropods within the inflorescences of *X. undipes* and *X. poeppigii* were recorded in the field, and were only collected when required for further identification. For each

TABLE 1. *Number and abundance per inflorescence and percent of occurrence from the total of sampled inflorescences for different taxa visiting three species of* Xanthosoma.

| | *Xanthosoma undipes* | | | | *Xanthosoma daguense* | | | | *Xanthosoma poeppigii* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Arthropods | No. ind./ Infloresc. | SD | Min–Max | Percent present | No. ind./ Infloresc. | SD | Min–Max | Percent present | No. ind./ Infloresc. | SD | Min–Max | Percent present |
| Acari | | | | | | | | | | | | |
| *cf.* Macrochelidae | | $+^{a,b}$ | | 40 | 2.4$^{c}$ | 7.2 | 0–52 | 38 | | $-^{d}$ | | 0 |
| Blattaria | | $-^{b}$ | | 0 | 0.02$^{c}$ | 0.16 | 0–1 | 2.8 | | $-^{d}$ | | 0 |
| Coleoptera | | | | | | | | | | | | |
| Dynastinae | | | | | | | | | | | | |
| *C. amblyopsis* | | $-^{b}$ | | 0 | 0.12$^{e}$ | 0.48 | 0–4 | 9.2 | | $-^{f}$ | | 0 |
| *C. gregaria* | | $-^{b}$ | | 0 | 0.52$^{e}$ | 0.86 | 0–5 | 35 | | $-^{f}$ | | 0 |
| *C. kaszabi* | | $-^{b}$ | | 0 | 0.002$^{e}$ | 0.05 | 0–1 | 0.3 | | $-^{f}$ | | 0 |
| *C. munda* | | $-^{b}$ | | 0 | | $-^{e}$ | | 0 | 0.13$^{f}$ | 0.72 | 0–4 | 3.4 |
| *C. sexpunctata* | 0.06$^{b,g}$ | 0.17 | 0–1 | 6.6 | | $-^{e}$ | | 0 | 0.03$^{f}$ | 0.18 | 0–1 | 3.4 |
| Nitidulidae | | | | | | | | | | | | |
| *M. costulata* | | $-^{b}$ | | 0 | 7.11$^{c}$ | 8.49 | 0–46 | 8.4 | | $-^{f}$ | | 0 |
| *M. straminea* | 0.16$^{b}$ | 0.58 | 0–3 | 10 | | $-^{c}$ | | 0 | | $-^{f}$ | | 0 |
| Curculionidae | | $-^{b}$ | | 0 | 0.56$^{c}$ | 1.05 | 0–5 | 28 | | $-^{f}$ | | 0 |
| Dytiscidae | 0.03$^{b}$ | 0.17 | 0–1 | 3.3 | 0.09$^{c}$ | 0.34 | 0–2 | 8.4 | | $-^{f}$ | | 0 |
| Staphylinidae | 0.03$^{b}$ | 0.17 | 0–1 | 3.3 | 0.07$^{c}$ | 0.42 | 0–3 | 2.8 | | $-^{f}$ | | 0 |
| Dermaptera | 0.1$^{b}$ | 0.39 | 0–2 | 6.6 | 0.7$^{c}$ | 1.08 | 0–7 | 46 | 0.36$^{f}$ | 1.31 | 0–7 | 14.2 |
| Diptera | | | | | | | | | | | | |
| Chironomidae (larvae) | 0.73$^{b}$ | 2.09 | 0–9 | 13 | 0.91$^{c}$ | 5.06 | 0–41 | 9.8 | | $-^{f}$ | | 0 |
| Psychodidae (larvae) | | $-^{b}$ | | 0 | 0.23$^{c}$ | 0.75 | 0–4 | 11.2 | | $-^{f}$ | | 0 |
| Drosophilidae | | $+^{b}$ | | | | $+^{c}$ | | | | $+^{f}$ | | |
| Syrphidae (larvae) | 1.4$^{b}$ | 3.9 | 0–16 | 16.6 | 1.94$^{c}$ | 2.03 | 1–11 | 100 | 0.57$^{f}$ | 1.26 | 0–4 | 17.8 |
| Hemiptera | | | | | | | | | | | | |
| Miridae | 8.5$^{2}$ | 9.5 | 0–22 | 50 | 0.19$^{3}$ | 0.7 | 0–4 | 8.4 | 0.53$^{6}$ | 1.23 | 0–6 | 28.5 |

[a] +,– presence–absence data.

[b] $N = 30$.

[c] $N = 71$.

[d] $N = 28$.

[e] $N = 348$: we included data on pollinator visits from García-Robledo *et al.* (2004).

[f] $N = 29$.

[g] *cf. sexpunctata*, voucher female, ID not certain without a male.

taxonomic group present in at least 5 percent of the sampled inflorescences (see Table 1), we tested for differences in the number of individuals present in inflorescences after different days of anthesis (*i.e.*, first, second, or third nights post-anthesis) by performing a Kruskall–Wallis test.

Additionally, to determine the composition and abundance of arthropods when pollination was successful, we collected developing infructescences of *X. undipes, X. daguense*, and *X. poeppigii*. Arthropods within the spathe tube in infructescences of *X. daguense* were collected and fixed in ethanol for further classification.

Vouchers of dynastine beetles were deposited in the Entomological Museum, University of Nebraska (Vouchers, CG *sn*, CG123 to CG128). Nitidulidae were deposited in the Louisiana State Arthropod Museum (Vouchers U124, RN114, RN64b, CG129 to CG135). Arthropods visiting *X. daguense* were deposited in the arthropod collection of the Instituto Humboldt—Colombia (temporarily held by Wildlife Conservation Society—Colombia Program).

## RESULTS

*Xanthosoma undipes* was visited by one species of dynastine beetle, *cf. Cyclocephala sexpunctata* (Table 1). In this species of *Xanthosoma*, 43 percent of the inflorescences displayed sterile flowers consumed by dynastine beetles ($N = 28$). The most common arthropods found inhabiting the inflorescences of *X. undipes* were mites, the nitidulid beetle *Macrostola straminea*, Dermaptera, and Miridae bugs (Table 1). We found chironomid larvae swimming within the mixture of pollen and water (Table 1), syrphid larvae were also frequently found feeding on the mixture of pollen and water at the bottom of the spathe tube (Table 1). Less frequent visitors include dytiscid and staphylinid beetles (Table 1). Aquatic beetles from the family Dytiscidae were only found in the oldest inflorescences (Table 1). The number of nitidulid beetles, mirid bugs, and Dermaptera within the spathe tube were similar during the first, second, and after the third night of opening (Table 2). We only found dipteran larvae in inflorescences only after the third night of opening (Table 2).

*Xanthosoma daguense* was visited by three species of dynastine beetles, *C. amblyopsis*, *C. gregaria*, and *C. kaszabi* (Table 1). We found evidence of dynastine visits in 33.6 percent of the sampled inflorescences ($N = 348$). The most common arthropods visiting the spathe tube of *X. daguense* include macrochelid mites, the nitidulid beetle *Macrostola costulata*, curculionid and dytiscid beetles, Dermaptera, and Miridae (Table 1). In this species of *Xanthosoma* we frequently found dipteran larvae such as Chironomidae, Psychodidae, and Syrphidae swimming in the mixture of pollen and water at the bottom of the spathe tube (Table 1). Less frequent visitors included *Trigona* bees, ants, cockroaches, staphylinid beetles, and undetermined Coleoptera larvae (Table 1).

In *Xanthosoma daguense*, the number of macrochelid mites, curculionid and nitidulid beetles, Dermaptera, and mirid bugs was similar during the first, second, and after the third night of opening (Table 2). We only found dytiscid beetles in inflorescences after the third night of opening. The number of Psychodidae larvae found was similar in inflorescences of different ages. Chironomidae and Syrphidae larvae were more abundant in older inflorescences (Table 2).

*Xanthosoma poeppigii* was visited by two species of dynastine beetles, *C. munda* and *C. sexpunctata* (Table 1). In this species, 25 percent of the inflorescences displayed evidence of visits by dynastine beetles ($N = 29$). The most common arthropods visiting *X. poeppigii* were Dermaptera, syrphid larvae, and mirid bugs (Table 1). For all taxa found in *X. poeppigii*, there was no difference in the number of individuals in inflorescences with different days of opening (Table 2).

The spathe tubes in infructescences of *X. undipes* were inhabited by chironomid larvae (Fig. 2). We did not observe nitidulid larvae or any signal of fruit predation in this species. *X. daguense* suffered fruit predation by nitidulid larvae. Infructescences in *X. daguense* also provided shelter for larvae of Diptera from the families Chironomidae and Psychodidae. Infructescences of *X. poeppigii* were not inhabited by arthropods (Fig. 2).

## DISCUSSION

*Xanthosoma daguense* and *X. undipes* displayed higher abundances and diversities of arthropods than *X. poeppigii.* Differences among *Xanthosoma* communities could be the product of differences in geographical distribution (Beaver 1983), differences in diversity and habitat heterogeneity among forests (Kitching 2000), sampling time or even characteristics intrinsic to the species such as inflorescence size (Seifert 1980) or abiotic factors such as pH conditions (Kitching 2000, Paradise 2000).

Despite this variation, the *Xanthosoma* species studied share some basic attributes. Resource availability in inflorescences comprised both allochthonous and autochthonous components. Allochthonous resources depend on nutrients dissolved in rainwater, and the amount of pollen brought during pollination. Autochthonous resources are produced by the inflorescence. These include sap consumed by mirid bugs, sterile flowers consumed by dynastine beetles, and the pollen produced by the same inflorescence. Heat produced by the inflorescence might also serve as reward to dynastines since it allows beetles to reduce their basal metabolism by 1/8 when mating and feeding inside the spathe tube (Seymour & Gibernau 2003).

The arthropods within inflorescence communities can be classified as sap feeders such as mirid bugs, pollen feeders such as nitidulids, curculionids, and syrphid larvae (C. García-Robledo, pers. obs.; Louton *et al.* 1996; Goldwasser 1987, 2000), and detritivores such as Dermaptera, chironomid, and psychodid larvae (Beutelspacher & Butze 1975, Goldwasser 1987, Louton *et al.* 1996, Kitching 2001*)*. Although dynastinae beetles feed on the belt of sterile flowers at the base of the spadix, they may also feed on pollen (Goldwasser 1987, 2000; Young 1986; C. García-Robledo, pers. obs). The role of mites in these inflorescence communities is not clear; they could be detritivorous or they may feed on floral exudates (Goldwasser 1987, 2000).

TABLE 2. *Numbers of the most common arthropods present in inflorescences of three species of* Xanthosoma *at different nights after opening.*

| | Nights after spathe blade opening | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | First | | Second | | Third | | | |
| | Mean | SD | Mean | SD | Mean | SD | df | $P^1$ |
| *Xanthosoma undipes* | ($N = 4$) | | ($N = 7$) | | ($N = 19$) | | | |
| Coleoptera | | | | | | | | |
| Nitidulidae | 0.75 | 1.5 | 0.14 | 0.37 | 0.05 | 0.22 | 2 | 0.4 |
| Diptera | | | | | | | | |
| Chironomidae (larvae) | 0 | 0 | 0 | 0 | 1.16 | 2.60 | – | $–^b$ |
| Syrphidae (larvae) | 0 | 0 | 0 | 0 | 2.2 | 4.70 | – | $–^b$ |
| Dermaptera | 0.25 | 0.5 | 0.29 | 0.75 | 0 | 0 | 2 | 0.14 |
| Hemiptera | | | | | | | | |
| Miridae | 12.5 | 9.5 | 14.5 | 9 | 5.4 | 8.90 | 2 | 0.05 |
| *Xanthosoma daguense* | ($N = 17$) | | ($N = 31$) | | ($N = 23$) | | | |
| Acari | | | | | | | | |
| Macrochelidae | 5.1 | 13.1 | 1.3 | 3.20 | 1.9 | 4.90 | 2 | 0.66 |
| Coleoptera | | | | | | | | |
| Curculionidae | 0.59 | 1.06 | 0.65 | 1.19 | 0.43 | 0.89 | 2 | 0.74 |
| Nitidulidae | 4.1 | 5.1 | 9.7 | 10.4 | 5.8 | 6.60 | 2 | 0.06 |
| Dytiscidae | 0 | 0 | 0 | 0 | 0.3 | 0.55 | – | $–^b$ |
| Dermaptera | 0.7 | 0.8 | 0.7 | 1.30 | 0.6 | 0.70 | 2 | 0.86 |
| Diptera | | | | | | | | |
| Psychodidae larvae | 0.41 | 1.0 | 0.1 | 0.53 | 0.3 | 0.76 | 2 | 0.18 |
| Chironomidae larvae | $0^{a,c}$ | 0 | $0.06^b$ | 0.25 | $2.74^b$ | 8.8 | 2 | 0.04 |
| Syrphidae larvae | $1.2^{a,c}$ | 0.6 | $1.5^{a,b}$ | 1.20 | $2.9^b$ | 2.90 | 2 | 0.03 |
| Hemiptera | | | | | | | | |
| Miridae | 0.29 | 0.84 | 0.13 | 0.49 | 0.22 | 0.85 | 2 | 0.80 |
| *Xanthosoma poeppigii* | ($N = 12$) | | ($N = 12$) | | ($N = 4$) | | | |
| Dermaptera | 0.66 | 2.01 | 0.16 | 0.38 | 0 | 0 | 2 | 0.68 |
| Diptera | | | | | | | | |
| Syrphidae larvae | 0.25 | 0.86 | 0.91 | 1.67 | 0.5 | 1.0 | 2 | 0.5 |
| Hemiptera | | | | | | | | |
| Miridae | 0.83 | 1.74 | 0.41 | 0.66 | 0 | 0 | 2 | 0.41 |

[a] Kruskal–Wallis test.

[b] Test not performed when only present in one of the categories.

[c] Significant differences between nights are indicated with different letters ($P < 0.05$).

In those phytotelmata in which a third trophic level was present (*i.e., X. undipes* and *X. daguense*), dytiscid beetles served as predators. It is also possible that Dermaptera, chironomid larvae, and staphylinid beetles may act as predators to some extent in these microecosystems (Seifert 1982, Kitching 2001). In treeholes, macrodecomposers such as scirtid larvae (Coleoptera) make resources available to microdecomposers (Paradise & Dunson 1997). In inflorescences of *Heliconia* (Heliconiaceae), bract feeding by *Cephaloleia* beetles (Chrisomelidae) also releases nutrients inside the phytotelm, thereby increasing the amount of resources available for decomposers (Seifert 1982). It is possible that in *Xanthosoma*, pollen feeders also increase the amounts of available resources to suspension and surface-feeding decomposers, acting as bottom-up facilitators.

Ants were infrequent visitors of *Xanthosoma* inflorescences and infructescences. A similar pattern was reported for one population of *X. undipes* in the tropical cloud forest of Monteverde in

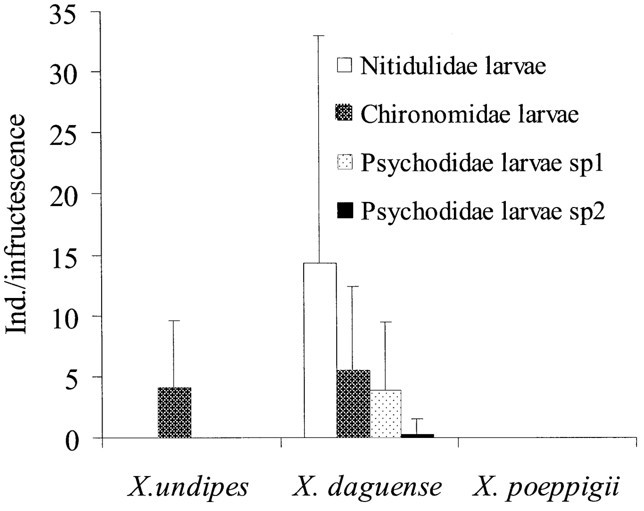

FIGURE 2. Number of Nitidulidae, Chironomidae, and Psychodidae (larvae) in infructescences of three species of *Xanthosoma* ($N_{X.undipes} = 15$, $N_{X.daguense} = 76$, $N_{X.poeppigii} = 12$).

Costa Rica (described as *X. robustum* in Goldwasser 1987, 2000, T. Croat, pers. comm.) and the dynastine-pollinated aroids *Philodendron aurantifolium*, *P. grandipes, P. pterotum*, and *P. radiatum* in the tropical lowland forest of La Selva Biological Station in Costa Rica (Goldwasser 1987). Phytotelmata in *Heliconia* are also infrequently visited by ants (Seifert 1982). However, inflorescences of the dynastine-pollinated Araceae *Philodendron platypetiolatum* are frequently visited by ants, who forage on extrafloral nectaries present on the spathe. In this species, the number of arthropods within the spathe tube is reduced by ant predation (Goldwasser 1987).

Arthropod succession in *Xanthosoma* starts early after inflorescences open. Inflorescences are initially colonized by adult terrestrial insects and syrphidae larvae arriving from adjacent inflorescences (Goldwasser 1987, 2000). A similar behavior is reported for syrphid larvae colonizing recently opened inflorescences of *Philodendron* (Goldwasser 1987), and bracts of *Heliconia* spp. (Seifert 1982). In *Heliconia*, plants female reproductive success could be reduced because hummingbirds, the main pollinators, avoid visiting flowers in bracts bearing syrphid larvae (Styles 1979). The effect of syrphid larvae on *Xanthosoma* reproductive success is unknown; however, these larvae could have a negative effect through pollen consumption, or a positive effect if they are able to prey on the eggs of seed predators such as nitidulid beetles (García-Robledo *et al.* 2004). Succession patterns could differ among *Heliconia* species at different localities. Bracts of *H. caribaea* on Puerto Rico Island are not initially colonized by syrphid larvae but by ceratopogonid larvae; as bracts age, inflorescences are colonized by psychodid and syrphid larvae (Richardson & Hull 2000). In older inflorescences of *Xanthosoma*, aquatic insects such as psychodid and chironomid larvae and dytiscid beetles increase in number. A similar successional pattern is reported for arthropod communities in *Heliconia*, in which aquatic taxa increase in number as bracts age (Seifert 1982).

In other aquatic microsystems, the permanence of a community depends, among other factors, on the fixed lifespan of the structure containing the community. In *Heliconia*, the lifespan of bracts can vary among species from 2 to 5 mo (Seifert 1982). In the Peruvian Amazonas, the aquatic macrofauna in the bamboo *G. weberbaueri* may inhabit internodes for 2–3 yr (Louton *et al.* 1996). In the pitcher plant *Nepenthes madagascariensis* (Beaver 1983, 1985), pitchers forming phytotelmata remain functional for *ca* 3 mo. In *Xanthosoma* inflorescences, permanence of the whole community inside the spathe tube depends on the arrival of and successful pollination by dynastine beetles. In *X. daguense*, the probability of abortion in unvisited inflorescences is three times higher than if the inflorescence is visited by at least one dynastine beetle, and abortion rate after the visit of one beetle is *ca* 50 percent (García-Robledo *et al.* 2004). If this abortion rate also occurs in *X. undipes* and *X. poeppigii*, at least 75 percent of the communities within inflorescences will only remain for few days. Another example in which the whole community depends on the arrival of one species in order to persist is phytotelmata in internodes of the bamboo *G. weberbaueri*. In this system, colonization starts only when the katydid *Leobliastes laevis* (Louton *et al.* 1996), or the weevil *Rhinantus latisternus* (T. L. Erwin, pers. comm.) bores a hole in the wall of the internode.

If pollination is successful, *Xanthosoma* fruits start to develop inside the spathe tube, and the community may persist for several months. Fruits ripen after *ca* 4 mo in *X. daguense* (García-Robledo *et al.* 2004) and *ca* 2 mo in *X. undipes* (described as *X. robustum* in Goldwasser 1987, T. Croat, pers. comm.). Within the infructescence there are two resources: detritus and developing fruits. In infructescences, all pollen consumers are absent, while only aquatic detritivorous such as psychodid and chironomid larvae are present. In *X. daguense*, we recorded fruit predation by nitidulid larvae. In this species, pupae and recently emerged adults of the nitidulid beetle *Macrostola costulata* are only present in near-ripened infructescences (García-Robledo *et al.* 2004). This suggests that the life cycle of this nitidulid beetle species is adapted to the flowering and fruiting cycles of *X. daguense*. Inflorescences of *X. undipes* in Costa Rica were also visited by one species of nitidulid beetle during flowering; however, infructescences did not display any sign of fruit predation. It is possible that fruit predation in this species is very minimal; therefore it was not recorded in the samples, or Nitidulidae do not oviposit inside the spathe tube of this species.

Some arthropods recorded in *Xanthosoma* phytotelmata were also reported in inflorescences of the dynastine-pollinated terrestrial aroid *Dieffenbachia nitidipetiolata* Croat & Grayum (described as *D. longispatha* in Young 1986, T. Croat, pers. comm.). Visitors of *D. nitidipetiolata* include *Drosophila* and Richardiidae flies, Miridae bugs, Dermaptera, and Thysanoptera. Spathe tubes in dynastine-pollinated vines from the genus *Philodendon* also can be filled with water, resulting in a sticky and viscous mixture of water and pollen (M. Gibernau, pers. comm.). Inflorescences of *Philodendron aurantifolium, P. grandipes, P. platypetiolatum, P. pterotum*, and *P. radiatum* are visited by Miridae bugs, Staphilinidae, Syrphidae larvae, earwigs, and thrips (Goldwasser 1987). Spathe tubes in vines of the genus *Syngonium* can also be filled with water, and may contain larvae of arthropods (T. Croat, pers. comm.). Further research may elucidate if phytotelmata similar to those described for *Xanthosoma* could occur among other dynastine-pollinated genera of Araceae, both in the understory and the canopy of Neotropical forests.

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